Vol. VII. *September, 1904.* *No. 4*

BIOLOGICAL BULLETIN

THE TEMPORAL ARCHES OF THE REPTILIA.

S. W. WILLISTON.

Students of herpetology are indebted to Professor Henry F. Osborn for a careful taxonomic and morphological study [1] of the extinct reptilia, from which he has concluded that the class is divisible into two distinct subclasses or phyla, which he has called the Synapsida and Diapsida. The writer has studied his paper with much interest and desires to acknowledge his indebtedness to it for many new ideas and stimulating suggestions, though he is forced to differ from the author in some of his conclusions. A full discussion of this paper is not possible at the present time, and the present communication, will, therefore, be restricted to a discussion of the relations of the bones of the temporal arches of the reptilia, relations which really lie at the basis of any classification.

I may mention, however, that I do not see my way clear to accept the term Synapsida proposed by Professor Osborn for the group of single barred reptiles, since this group really does not differ in any essential respect from the Synaptosauria (in the wider sense) of Fürbringer [2] and differs from the Synaptosauria of Cope, as most recently defined by him [3] chiefly in the inclusion of the Cotylosauria. But, I believe that Cope was right in separating the two groups, since he recognized, as does Osborn, the ancestral relations of the Cotylosauria to both the single and double-barred reptiles. If all other reptiles are derived from them, and

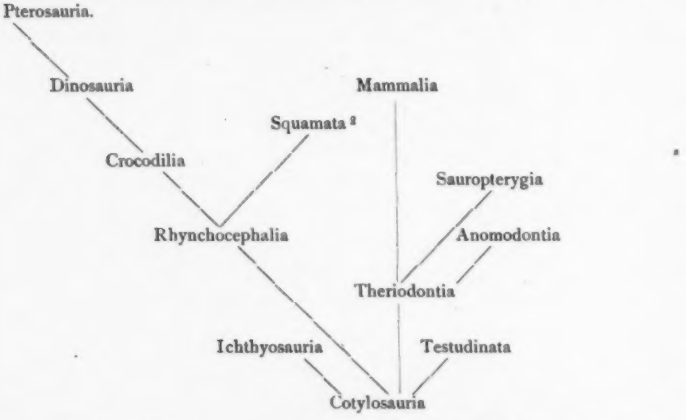
[1] "The Reptilian Subclasses, etc." *Mem. Amer. Mus. Nat. Hist.*, Vol. I., p. 451, 1903.

[2] *Jena Zeitschr.*, 1900.

[3] "The Crocodiles, Lizards and Snakes of North America," Rep. U. S. Nat. Mus., 1898, p. 159.

if the differences of these reptiles are sufficiently great to separate them into distinct orders, it would seem proper to distinguish the Cotylosauria from both the Synapsida and the Diapsida. Indeed Professor Osborn himself excludes them from union with either group in some of his definitions.

Furthermore, I cannot accept the conclusion as definitely proven, or even probable, that the reptiles are really diphyletic. The turtles seem, with much reason, to have had an independent origin from the cotylosaurs. My views in general of the pylogenetic relations of the orders of reptiles are pretty well expressed in the following diagram published by Cope in 1896.[1] It will be



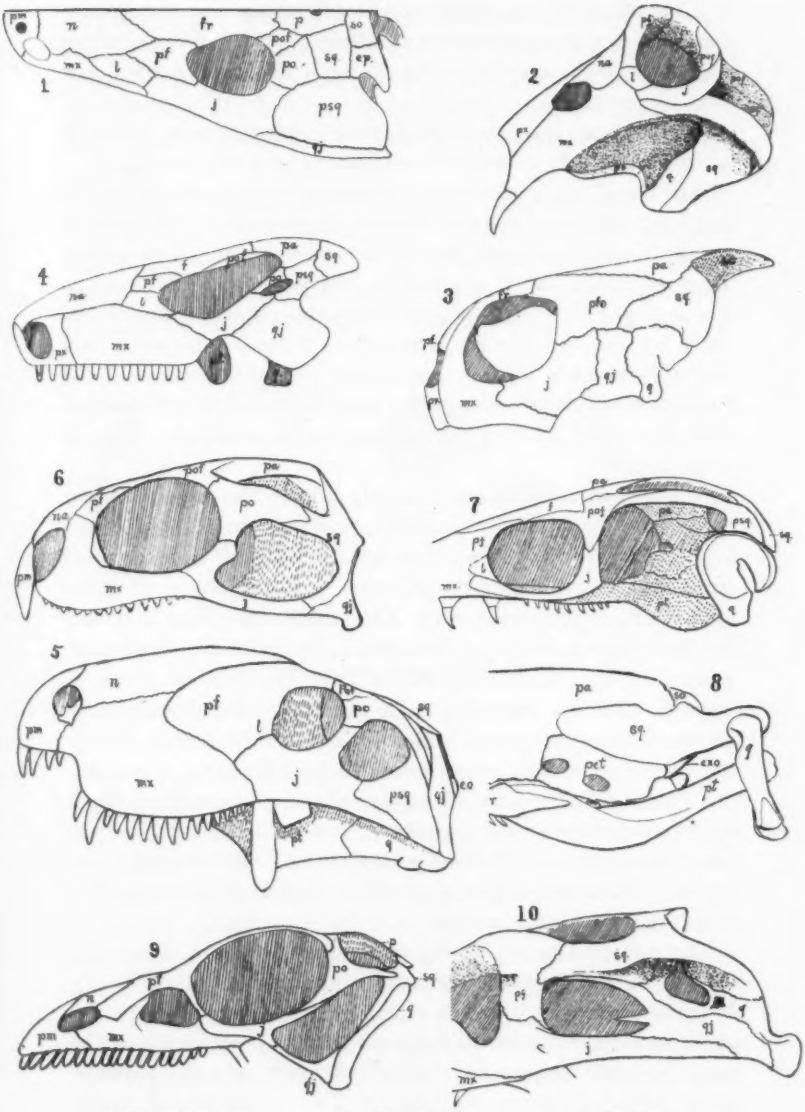
seen that, with the exception of the Ichthyosauria and Testudinata, the phylogeny scarcely differs from that of Professor Osborn, save in details. Osborn's characters are as follows:

Synapsida. — "A single large supratemporal fenestra; latero-temporal fenestra rudimentary or wanting. Bony elements of upper and lower arches not separated. Upper arch tending to degenerate first.

"Squamosals and prosquamosals large, expanded, early coalesced, forming a portion of the occiput, suturally covering the quadrate, secondarily entering the glenoid fossa.

[1] "Primary Factors of Organic Evolution," p. 115.

[2] "It is uncertain whether this order originated from the Theriodontia or the Rhynchocephalia." In the original it is derived from the Theriodontia.



1. *Mastodonsaurus*,
2. *Lystrosaurus*,
3. *Chelone*,
4. *Procolophon*,
5. *Dimetrodon*,
6. *Sphenodon*,
7. *Platecarpus*,
8. *Python*,
9. *Anchisaurus*,
10. *Gavialis*.

Diapsida.—" Large supra- and laterotemporal fenestræ ; laterotemporal fenestra sometimes secondarily closed. Bony elements of arch widely separated. Lower arch tending to degenerate first.

"Squamosals and prosquamosals often reduced, more generally separate, partially covering or withdrawn from the quadrate."

The closed or nonfenestrate condition of the temporal region has long been recognized as a primitive character in the reptilian skull. Cope, Baur and Seeley, and other authoritative writers have repeatedly called attention to the striking resemblances in the arrangement of the bones forming this region in some of the early reptiles and the Stegocephalia. Largely because of this resemblance some authors have urged the reptilian nature of the Stegocephalia, either uniting them with the reptiles as a branchiate division of the class, or placing them in a distinctive class, as " Proreptilia."

While these elements are so nearly alike in the stegocephs and cotylosaurs as to leave no doubt of their homologies, in the higher or more specialized reptiles the changes have been so great that the identification of some of the bones is doubtful. As a result of this uncertainty, many names have been proposed for the different temporal elements, aside from the postfrontal, postorbital and jugal, about which there has been no doubt or dispute. For the other four bones, however, I find the following names in use within recent years : epiotic, os tabulare, paroccipital plate, squamosal, prosquamosal, suprasquamosal, supratemporal, mastoid, supramastoid, supraquadrate, paraquadrate, zygomatic, quadratojugal, squamosal I., squamosal II. At the present time, the terms squamosal, prosquamosal, quadratojugal and epiotic seem to have most acceptance, though supratemporal is largely used for prosquamosal.

The temporal bones in the Stegocephalia and Cotylosauria are practically identical in number and arrangement (Figs. 1, 11). In both these forms it will be observed that the squamosal articulates broadly in front with the postorbital or postfrontal ; on the inner side with the parietal ; on the outer side with the prosquamosal, and sometimes the jugal. The prosquamosal unites broadly in front with the jugal ; on the outer side with the

quadratojugal. The quadratojugal has only a slight union with the jugal. The postfrontal joins by its whole length with the parietal. Now, no one will question but that this arrangement of these bones is the primitive one for the reptilia, and any rearrangement or readjustment must be a secondary result or specialization.

Among the higher forms, the nearest approach to this condition is seen in the testudinate skull (Fig. 3), in which the bony roof still remains unpierced; that is, there is no supra- or latero-temporal fenestra in such forms as *Chelone*, an undoubted primitive type of testudinate skull. The postorbital and postfrontal

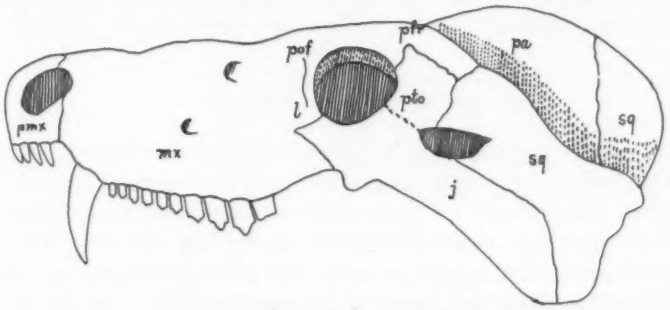


FIG. 14. *Cynognathus*, after Woodward.

are not distinct, or one or the other is absent. The prosquamosal has disappeared, or has become fused with some adjacent element. The quadratojugal has become greatly enlarged, separating the jugal from the quadrate, and articulating above with the squamosal — that is, it has taken the position of the prosquamosal in the *Pareiasaurus* skull. It is assumed that the prosquamosal, if present, is fused with the squamosal, but I fail to see any conclusive evidence of this; and it would seem more reasonable that, if the element is really present in the testudinate skull, it is fused with the quadratojugal, which has usurped its place and relations. Indeed the loss of the narrow bone on the outer side of the cotylosaurian skull would leave an arrangement pretty similar to that of *Chelone*, except that the quadrate is partly uncovered.

In the posterior part of the skull a vacuity has arisen, or, more

probably, was inherited from the cotylosaurs, between the parietal, paroccipital and squamosal, the posttemporal vacuity. By an emargination of the roof from behind, the squamosal may become separated from the parietal, and by an emargination from below,

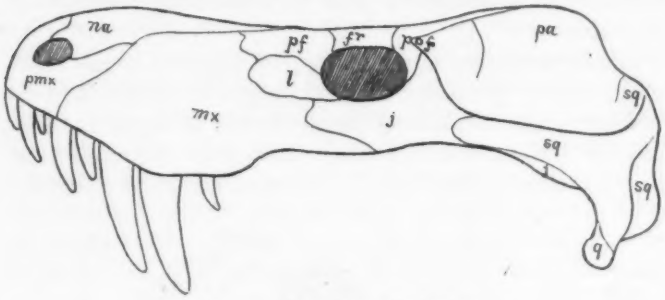


FIG. 12. *Lycosuchus*, after Broom.

from the postorbital, indeed, entirely isolating it in the arch. In such cases a large fossa is disclosed from above, which is sometimes, *though incorrectly*, called the supratemporal fossa. Baur some years[1] ago called attention to the fact that the turtles have no supratemporal fossa or fenestra. In fact, the temporal roof of the turtles throughout seems to be quite like that of the cotylosaurs, judging from Seeley's description:[2] "While the temporal vacuities are roofed over in *Pareiasaurus*, the roof is like the primitive roof of the genus *Chelone*, whereas in Professor Cope's figures of *Empedias* the skull appears to be closed behind as in Gorgonopsia." That the turtles ever had a supratemporal fenestra is quite out of the question. How, then, is it possible to derive them from the Anomodontia (*sens. lat.*), or from any known group of reptiles save the Cotylosauria? The entire absence of the quadratojugal bone, or any ossification corresponding to that bone in the Testudinata, in all the Anomodontia, Theriodontia, Placodontia and Therocephalia is exceedingly difficult to explain, if they are ancestral to the turtles. Has this bone reappeared, after its loss or close fusion with other bones? I am aware that many attempts have been made to show the relation-

[1] *Jour. Morph.*, iii., p. 472, 1889.
[2] *Phil. Trans.*, 1894, p. 1009.

ship of the turtles with the placodonts and plesiosaurs, but a study of these forms convinces me that whatever resemblances they may present can be accounted for by parallel development. Briefly, there are other characters in the skeleton that seem inconsistent with such a derivation from the Anomodontia, the intercentral attachment of the ribs, the presence of parial intercentra in the cervical vertebræ of some forms, etc. The conclusion seems irresistible to me that the Testudinata represent a distinct phylum of the reptilia, coördinate with the Synaptosauria or Synapsida.

By a sort of natural trephining of the skull-wall, a vacuity appeared between the squamosal and parietal, the squamosal still retaining its connection posteriorly with the parietal, and the

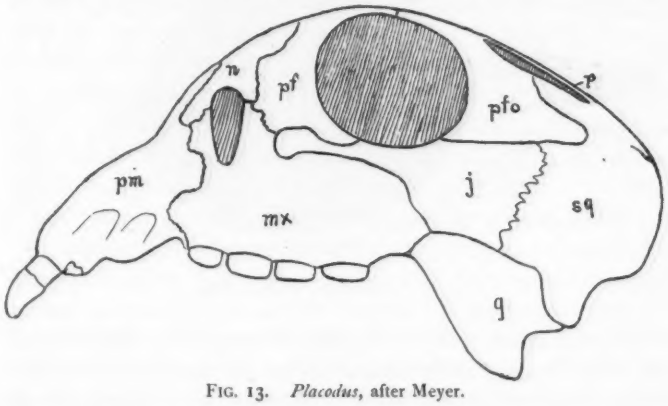


FIG. 13. *Placodus*, after Meyer.

postorbital taking a part in the separated bar thus formed. This is the condition in the Anomodontia and Sauropterygia, but never in the Testudinata. In the Anomodontia and Sauropterygia, concerning whose relationships there can be no doubt, the prosquamosals and quadratojugals have disappeared, leaving a single bar composed of the squamosal, postorbital and jugal. It is also assumed here that the prosquamosal and perphaps also the quadratojugal have become fused with the squamosal, but of this there is not a scintilla of evidence. A separate ossification, it is true, has been said to occur in some plesiosaurs by Owen,[1] which

[1] *Trans. Geolog. Soc. Lond.* (2), V., pt. iii., pl. XLV., 1840.

might be supposed to be the prosquamosal, but in the excellent skulls of four genera of these animals which I have examined there is positively no such separate element present, nor was there any recognizable prosquamosal present in the skulls described by Andrews. Nor has such an element ever been recognized in the Nothosauria. I am aware that Koken[1] has suspected the presence of such an element in one specimen of a nothosaur, but his evidence was very doubtful and has not been confirmed. I am confident that the true squamosal in these groups, as in the cotylosaurs and turtles, articulates directly with the post-

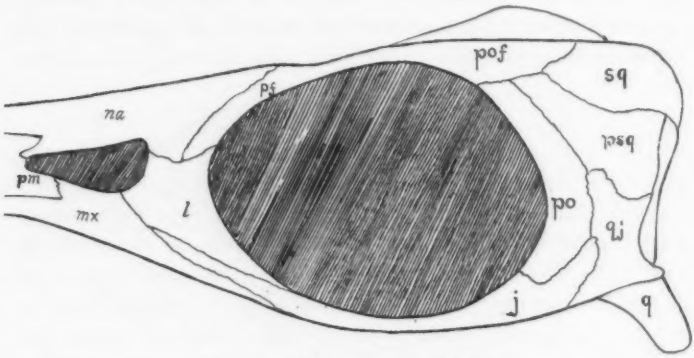


FIG. 17. *Ichthyosaurus*, after Owen.

orbital and jugal, without the intervention of any other element, and that the prosquamosal is wanting, not fused with adjoining bones; nor is there any certain evidence of the presence of the quadratojugal in any of these reptiles. In certain plesiosaurs I have found and figured what I believed to be a distinct ossification — a small, perhaps rudimentary one — that I took to be the quadratojugal. But I have never been able to trace it out, and no other observer has ever distinguished this element in the Sauropterygia. In the Anomodontia no such element has been certainly found, and, since we have the best of reason for believing that the anomodonts and theriodonts are closely related to the ancestors of both the nothosaurs and the plesiosaurs, we can hardly expect to find the bone distinct in these latter forms.

[1] *Zeitschr. Deutsch. Geolog. Gesellsch.*, XLV., 1893; p. 362.

Since the above was written, I have received the following statement from Dr. Broom, kindly sent in reply to a query from me: "No trace of either prosquamosal or quadratojugal has been found in any Anomodont or Theriodont. The large bone which supports the quadrate in *Dicynodon* and also forms so large a part of the temporal arch is all pure *squamosal.* The same is the case in the Therocephalia and Theriodontia. The upper part of the quadrate which rests on the squamosal has been thought by some to be the quadratojugal, but I am pretty confident that the whole is quadrate, and that no rudiment even of the quadratojugal is present."

From these facts we may conclude that the emargination of the single bar has removed all of the lower arch, and that all which remains corresponds to the upper arch of the diapsid reptiles, the squamoso-postorbito-jugal bar. Certainly until some form is discovered in which the prosquamosal and quadratojugal are definitely shown to be present as a part of the arch, the compound nature of the arch in the synapsid forms is hypothetical. One species of *Cynognathus* has been figured (Fig. 14) with a small fenestra between the squamosal and jugal. No other species of this genus possesses this opening, and its presence in this species, is, I believe, disputed by Dr. Broom. Even if it be present, it has no classificatory significance, since it must have been a parallel development in these animals; an abortive attempt, as it were, without phylogenetic significance. It is of interest, perhaps, if it really occurs in any of the anomodonts, as showing the tendency to perforation of a broad plate covered on both sides by muscles.

The question is properly asked: How has the mammalian zygoma arisen? The answer does not seem doubtful to me. The mammalian arch has the structure of that of *Lycosuchus* (Fig. 12), and is composed of the squamosal and jugal alone. This it seems to me, will be made apparent by the consideration of the arch in *Placodus* (Fig. 13), *Cynognathus* (Fig. 14), and *Lystrosaurus* (Fig. 2), in which the articulation of the squamosal is with both the postorbital and the jugal in about equal measure.[1]

[1] "I can find no difference in the character of the arch in the Anomodontia and Theriodontia except that in the Theriodont the malar bone has a greater external back-

In all the plesiosaurs (Fig. 16) the union of the squamosal with the postorbital has become much reduced, they merely touching each other and approaching the theriodont type, in which the postorbital has become wholly separated from the squamosal (Fig. 12).

The assumption that the prosquamosal or quadratojugal has thrust itself up between the squamosal and the postorbital is gratuitous, without evidence to support it. And, if they have not been thrust upward into this intercalary position, it must be assumed, if the bones are really present, that they form the lower part of the bar, parallel with the squamosal, intercepting the jugal from union with the squamosal. That the jugal may unite with the squamosal, even when the prosquamosal exists as

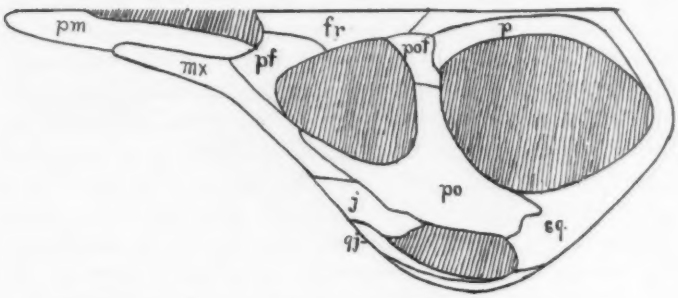


FIG. 15. *Stenometopon*, after Boulenger.

an independent ossification, is a fact, as is shown by the structure in the cotylosaur skull. Why then is it necessary to assume that these bones, or either of them, are present in the anomondonts and sauropterygians in a fused condition?

It is of course possible that the quadrate has also become a part of the mammalian arch, as has been urged by Dollo, Albrecht, Baur and others. The extraordinary development of the squamosal bone in the anomodonts and theriodonts has not only crowded out the prosquamosal and quadratojugal, but has also caused the absorption of the quadrate, enclosed between it and

ward development than is usually seen in the Cynodontia; but the difference between the groups is not due to any difference in the nature of the arches, but to a less development of the quadrate bone in the Theriodontia, which has resulted in a diminution or atrophy of the descending pedicle of the squamosal bone" (Seeley, *Phil. Trans.*, 1894, p. 997.)

the skull wall, the squamosal taking its function as an articulating bone for the lower jaw. I see no urgent reason for insisting that a vestige of it must yet be present in the eutherian skull, either as a part of the zygomatic arch, or in a totally different function as one of the ear bones. We are quite sure that some of the bones of the reptilian skull are not present in the mammalian skull, why may not the quadrate be one of them? There seems to be an idea that bones of the reptilian skull can only become lost by their union with contiguous bones, their ossific centers finally disappearing. But I am skeptical of this. We know that the quadratojugal is not present in the Squamata; that the 'prosquamosal' of the arched lizards is not present in

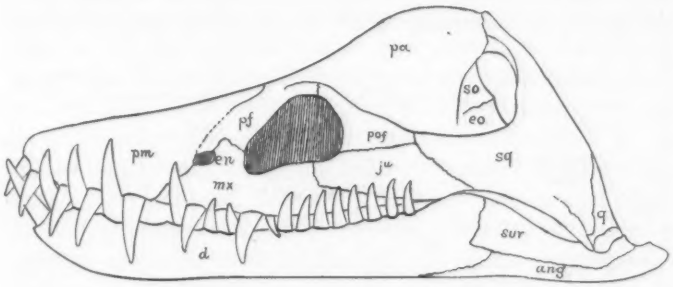


FIG. 16. *Cimoliasaurus*, original.

the amphisbænians or snakes; that the epipterygoid is also wholly wanting in some of the lizards, as well as other bones. Must we insist that their loss has always been by fusion and loss of ossific center? Must we insist that the lachrymal bone is always present in the turtles, snakes and *Sphenodon*; that the jugal is still a part of the postorbital or maxilla of the snakes; that the prevomers still remain as a part of some other bones in the eutherian mammals; that the splenial and coronoid still remain in the mammalian mandible?

Turning now to the double-barred or diapsid forms, it is a question which of the two vacuities appeared first, or whether they did not appear together. In *Ichthyosaurus* and *Aëtosaurus* we have a single vacuity, but the relations of both these forms are so evident with the early rhynchocephaloid reptiles that

there is perhaps good reason for the belief that the original lateral fenestra in the icthyosaurs has become closed up by the posterior obtrusion of the orbit, as was suggested by McGregor. That this was really the case, however, has by no means been proven. We can conceive of an early diapsid stem without lateral fenestration (as is indeed the case, in *Procolophon*), from which the ichthyosaurs might have been derived. Certainly the Ichthyosauria are the most primitive of reptiles, save the cotylosaurs, in so far as the lateral temporal region is concerned. The squamosal and postfrontal here form the outer boundary of the supratemporal vacuity, while the large prosquamosal is intercalated between the squamosal, postorbital and quadratojugal. If the ichthyosaurs originally had a latero-temporal fenestra it was situated, in all probability, above the prosquamosal. (Fig. 17.)

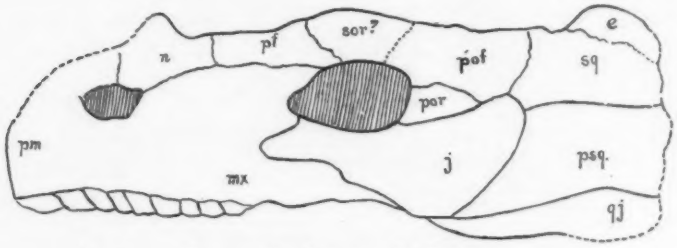


FIG. 11. *Parciasaurus*, after Seeley.

Next to the ichthyosaurs, the most primitive of the diapsid types, as urged by Broom and Osborn, seems to be *Procolophon*. (Fig. 4). Here there is a peculiar arrangement of the bones of posterior region. A slender one by the side of the frontal and parietal, above the orbital opening, must be the postfrontal; while another bone articulating with the parietal and jugal, situated below and behind the eye cavity, is as certainly the postorbital. The orbit, we may conclude, has been extended backward, not by the closing up of the laterotemporal vacuity, but by the absorption of the postfrontal and postorbital, so as to come into contact with the parietal between them. But the orbit does not include the supratemporal vacuity, since neither the postorbital nor the squamosal helps form its outer boundary. There

is no evidence, in my opinion, that the large eye-opening has been formed by the coalescence of the supratemporal and orbital vacuities, but rather by the extension backward of the orbit, through the absorption of the postorbital bones. At the posterior part of the skull is seen an element which was believed by Seeley[1] to be the epiotic, a bone otherwise unknown, save possibly in some anomodonts, in the higher reptilia. Woodward,[2] however, identifies this bone as the squamosal, and the so-called squamosal in front of it he cails the prosquamosal. I do not feel at all sure which view is correct. If the two elements are really the epiotic and squamosal of the cotylosaur skull, I fail to understand how *Procolophon* could have stood in any very intimate relations with the early rhynchocephaloid reptiles, for they primitively had a prosquamosal. Professor Osborn states that all the elements of the cotylosaur skull are present in *Procolophon*, but neither his figure, nor Seeley's nor Broom's descriptions indicate the presence of all three bones, the epiotic, squamosal and prosquamosal — one of these elements seems certainly to be absent. Between the postorbital and the squamosal, there is a small vacuity shown in the original figure of this reptilian skull, the one reproduced here, which has been believed to be the laterotemporal fenestra. But, if I am correct, Dr. Broom denies the presence of this opening, and the figure he has been kind enough to send me shows no laterotemporal vacuity, in that position at least. Are we to suppose, such being the case, that, in addition to the absence of a supratemporal vacuity, the lateral opening also has been closed up secondarily? It seems to me that such reasoning savors a little too strongly of the ante-Baconian methods.

While *Procolophon* is shown by Broom, from certain evident peculiarities of the skull and skeleton to be more nearly related to the Rynchocephalia than to the Anomodontia, I fail to see any striking resemblances in the temporal region. It is a diapsid without temporal fenestræ.

Perhaps the most primitive known of the truly rhynchocephaloid type of reptiles, so far as the temporal region is concerned,

[1] *Phil. Trans.*, 1889, p. 271. "It rests by a squamous overlap upon the posterior border of the squamosal, and the external surface of the parietal."

[2] "Vertebrate Paleontology," p. 149, Fig. C.

is the Pelycosaurian *Dimetrodon* (Fig. 5) from the Permian of Texas, recently fully made known by Professor Case.[1] Here we have, in addition to the fully developed superior opening, a large fenestration below the squamoso-postorbital bar, and bounded below by the jugal and prosquamosal. The quadratojugal is relatively small, intercalated between the prosquamosal and the quadrate, and wholly separated from the jugal. *Paleohatteria* may possibly have a separated prosquamosal in the same position and with the same relations, but this fact, if fact it is, is yet to be determined. The Triassic *Hyperodapedon* and the allied *Stenometopon* (Fig. 15) have no separated prosquamosal. *Saphæosaurus*, from the Jurassic, more nearly ancestral, perhaps, to the modern *Sphenodon*, in all probability possesses a separated prosquamosal intercalated between the quadratojugal and the jugal, as in *Dimetrodon*. Finally in the living *Sphenodon*, notwithstanding its many primitive characters, the prosquamosal has utterly disappeared, even in the embryo, according to Howes and Swinnerton, though the squamosal is continued above the quadratojugal to unite with the jugal (Fig. 6). Here the quadratojugal articulates with the jugal, as in all the archosauria, the intervening bone having disappeared. Baur[2] believed that the prosquamosal was present in *Sphenodon* though early fused with the squamosal, a view which now is shown to be incorrect. The bone has been gone so long that it fails to make any impression upon the embryo.

From all of which evidence, *Dimetrodon*, *Saphæosaurus*, possibly *Paleohatteria*, and the conditions now existing in *Sphenodon*, the conclusion is irresistible that the laterotemporal vacuity was originally formed in the true diapsid reptiles not below, but above the prosquamosal; that this bone has nothing to do with the upper bar in these reptiles, which without exception was formed primitively by the squamosal and postorbital; secondarily by the squamosal, postorbital and jugal; finally in the theriodonts and mammals by the squamosal and jugal alone. The prosquamosal never forms the outer margin of the supratemporal fossa.

All this leads us to the consideration of the arch in the Squamata wherein the condition of things has caused no end of con-

[1] *Journal of Geology.*

[2] *Anat. Anzeiger*, X., p. 321, 1895.

troversy and differences of opinion, differences which are by no means yet settled. The single arch present (Fig. 7) has been variously considered to be the lower arch, the upper arch, or a compound of both arches. It is composed (when present) of three bones; an anterior one, the postorbital, extending backward to unite with a middle one; the middle one joining the postorbital in front, the posterior one and often the parietal behind, and more or less broadly articulating with the upper end of the quadrate; and a posterior element, joining the parietal internally, the middle element anteriorly, and united with the petrosal and exoccipital below, and usually also articulating with the head of the quadrate. The middle bone has been called the temporal, squamosal, quadratojugal, prosquamosal, supratemporal, zygomatic, supramastoid, paraquadrate; the posterior element, the mastoid, squamosal, supratemporal, supramastoid, and paroccipital. At present most writers, following Baur,[1] call the middle element the prosquamosal, and the posterior one the squamosal, though Woodward[2] applies the name squamosal to the middle element, and supratemporal (prosquamosal) to the posterior one.

It is now generally assumed that the Squamata have descended from the rhynchocephaloid reptiles. We have seen that in the early diapsid reptiles the prosquamosal is not articulated between the squamosal and the postorbital, but forms a part of the lower arch between the quadratojugal and the jugal. Here, however, it is assumed that the lower arch of the rhynchocephs has disappeared, that the quadratojugal is lost, but that the bone articulating with the quadratojugal between it and the jugal has been transferred to the upper arch, a position unknown in any other reptile, recent or extinct, to bound the outer part of the supratemporal vacuity. One could with as much reason call it the quadratojugal with former authors and with Baur[3] when he believed that the Squamata were not closely related to the rhynchocephalians, and that the arch of the Squamata was formed, not by the loss of the lower arch, but by the fusion and attenu-

[1] *Anat. Anzeiger*, X., p. 328, 1895.
[2] "Vertebrate Paleontology," p. 143, Fig. E; p. 192, Fig. A, 1898.
[3] *Journ. Morphology*, III., 473, 1889.

ation of a compound arch. One thing seems very probable, if this bone is the prosquamosal, then the Squamata have nothing to do with the rhynchocephaloids, but represent a separate and distinct phylum of their own. I prefer to call the bone articulating with the postorbital the squamosal, the bone which in all other reptiles articulates with the postorbital behind.

Of course, if this is the real squamosal, the posterior element cannot be a squamosal, though Koken [1] thought to solve the difficulty by calling the two bones squamosal I. and squamosal II. The history of the contention between Cope and Baur [2] as to the identity of this bone is too fresh in the minds of anatomists to need repeating here. Baur vigorously urged that the bone at the end of the suspensorium is the squamosal, but Baur never fully understood the relations of this bone in the mosasaurs, as is evidenced by his faulty description of it.[3] As Cope has repeatedly affirmed,[4] and as I have confirmed,[5] the so-called squamosal of the mosasaurs is intercalated between the exoccipital and petrosal, extending far inward nearly to the surface of the braincase. It needs but a moment's consideration by any one familiar with the relations of the bone in these animals and in the mammals to be convinced that such remarkably different conditions cannot be those of the same bone. The inner part of the "squamosal" corresponds quite well with the outer part of the paroccipital, or opisthotic element, which was not found in the lizard embryo by Parker. Referring now to the figures of *Procolophon* and *Pareiasaurus*, it will be seen that the outer part will correspond fairly well with the one called the epiotic. "In some of the genera of Stegocephalia the paroccipital is free from the exoccipital; in others (*Mastodonsaurus*) it is coössified with the exoccipital. The paroccipital is in relation to a dermal plate which is very improperly called the epiotic. I propose the name '*paroccipital plate*' for it." [6] It may be objected that the presence of an epiotic bone in the lizards is a far too primitive char-

[1] *Zeitsch. Deutsch. Geol. Gesellsch.*, XLV., p. 363, 1893.
[2] *Amer. Nat.*, 1895, 1896.
[3] *Jour. Morphology*, VII., p. 14, 1892.
[4] *Trans. Amer. Phil. Soc.*, XVII., p. 19, 1892.
[5] *Univ. Geol. Surv. Kans.*, IV., p. 121, 1898.
[6] Baur, *Journ. Morph.*, III., p. 469, 1889.

acter, but we are now quite certain that the lizards are an exceedingly old group, probably dating from the Permian, and that they have not a few very primitive characters, such as the presence of pterygoid teeth; perhaps the early forms, like those of the early crocodilia, will all be found to have amphicœlous vertebræ. However, whether or not this outer plate has early fused with the paroccipital beneath it, and has remained persistent in the lizards, I will not say, but I do believe that the bone corresponds to the paroccipital.

The archosaurian type of arches is one easily derivable from the Rhynchocephalia — a conjoined postfrontal and postorbital uniting posteriorly with the squamosal, to form an upper bar; and a quadratojugal intercalated between the jugal and quadrate to form the lower bar. The variations in the dinosaurs (Fig. 9) and the crocodiles (Fig. 10) are not great, and doubtless a like structure will be found in the pterosaurs when this part of their anatomy is better known than it is at the present time.

Returning now to the theses which headed this discussion, we see: That, in the Synapsida, neither the Cotylosauria nor the Testudinata have a large or any supratemporal vacuity; that, the cotylosaurs, if ancestral to the Synapsida, the Diapsida and the Testudinata, cannot be properly included into a subclass with any one of them; that the turtles could not have been derived from the Anomodontia, but apparently represent a distinct and independent branch from the Cotylosauria, or at the least from the primitive stem of the Synapsida before it had developed a supratemporal fenestra; that there is no evidence of a prosquamosal bone in any of the Synapsida (excluding the cotylosaurs), and little of the quadratojugal in the Anomodontia and Sauropterygia; that it was the elements of the lower, not the upper arch which became degenerate, leaving the mammalian zygoma to be composed of the squamosal and jugal only.

That, in the Diapsida, the prosquamosal is known to be present in but two forms; that it was an element of the lower, not the upper arch; that the arch of the lizards is the upper, not the lower one, and consequently does not contain the elements of that arch; that *Procolophon*, though a primitive diapsid, had

neither upper nor lower temporal fenestra, and probably never had.

These, it seems to me are legitimate conclusions from the evidence now available. But the evidence is yet meager, and all our present views may undergo material modification when more of the early reptiles from the Trias and Permian are known.

EXPLANATION OF FIGURES.

ep., epiotic.
exo., exoccipital.
fr., frontal.
j., jugal.
l., lachrymal.
mx., maxilla.
n. or *na.*, nasal.
p. or *pa.*, parietal.
pf., prefrontal.
pm., premaxilla.
pof. or *pfr.*, postfrontal.
po., or *pto.*, postorbital.
psq., prosquamosal.
pt., pterygoid.
q., quadrate.
qj., quadratojugal.
so., supraoccipital.
sq., squamosal.

In Fig. 4, *Procolophon*, the determination of the squamosal and prosquamosal is that of Woodward. According to the interpretation of Seeley, Broom and Osborn, *sq.* is the epiotic, *psq.* the squamosal. I am under obligations to Prof. Case for permission to use his figure of *Dimetrodon* in advance of publication by him.

FORM-REGULATION IN CERIANTHUS, VI.

Certain Special Cases of Regulation and their Relation to Internal Pressure.

C. M. CHILD.

In this paper are described certain regulative phenomena of interest both from a descriptive point of view and because they appear to offer further evidence upon the problem of the rôle of internal water-pressure in regulation. At present I can see no other satisfactory interpretation of these cases than that based upon internal pressure. In any case, however, they are interesting modifications of the typical course of regulation and as such deserve mention.

The Oral Regeneration of Oblique Pieces.

Pieces with oblique ends are obtained by sectioning the body at various angles to the principal axes as indicated in Fig. 1. Such pieces show a very marked difference in rapidity of regeneration on the different parts of the oblique cut surface, regeneration being most rapid on that part which represents the region nearest the oral end of the parent body and least rapid on the opposite side. This difference is due in part to the fact discussed in my second paper ('03*b*), viz., that the rapidity of regeneration always decreases with the increasing distance of the regenerating surface from the oral end of the original animal. But the difference in the rapidity of regeneration on the different parts of the oblique surface is considerably greater than that between control pieces with transverse cut surfaces at corresponding levels. It follows from this that some other factor in addition to the difference of level is concerned in the result.

Before proceeding to the description of experiments it should be said that the possible significance of oblique pieces was not fully recognized during the course of my experiments, therefore my study of such pieces was less extended than it would otherwise have been. The data are sufficient, however, to show

clearly the consequence of cuts of this kind. *C. solitarius* was used for those experiments.

Series 9.

September 12, 1902.— Three specimens of *C. solitarius* were cut obliquely at two different levels as indicated in Fig. 1; the pieces used for experiment in each case being the portions between the two oblique lines. These pieces possessed an oral and an aboral oblique surface. Unfortunately no control pieces with transverse cut surfaces were made but the records in my notes of a set of pieces which were cut at the same time and kept in the same aquaria will serve as controls. These pieces were prepared as

FIG. 1.

FIG. 2.

follows: after the removal of the oral end from two specimens by means of a transverse cut just aboral to the œsophagus the remaining portion of the body was cut into three equal pieces (Fig. 2). These pieces may be designated as *A*, *B*, and *C*, *A* being the most oral of the three. By comparison of Figs. 1 and 2 it is seen that the oral end of the control piece *A* is at almost the same level as the most oral portion of the oblique piece, the latter being slightly more oral, while the oral end of piece *B* corresponds very closely in level with the most aboral portion of the cut surface of the oblique pieces. In sectioning living animals so con-

tractile and changeable in form as *Cerianthus* the correspondence between the levels of cuts on different specimens is always only approximate. In this case the levels at which the oblique cuts were made differ more or less in the three specimens as well as the levels of the transverse cuts in the controls. Any control is therefore only approximate and the pieces used for this purpose here are as satisfactory in this respect as those employed in other experiments on *Cerianthus*.

In the control pieces *A* and *B* the rapidity of regeneration is that characteristic of the level of the body at which the oral ends of the pieces lie. Comparison of this rapidity with that of the extreme levels of the oblique cut surfaces will show whether the obliquity of the cut has any effect on the rapidity of regeneration.

FIG. 3.

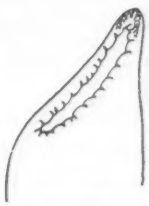


FIG. 4.

After the operation the collapsed oblique pieces acquired a form like Fig. 3. During the next day or two the cut edges rolled inward still more closely and the pointed oral portions became more or less bent over toward the cut surfaces. All became more or less flattened as they lay upon the flat glass bottom of the aquaria.

September 15. — 3 days after section. Experimental pieces: One piece with a few minute tentacle-buds at the uppermost portion of the oblique cut surface; others without tentacles.

Controls. All without tentacles.

September 17. — 5 days after section. Experimental pieces: All the pieces were completely or nearly closed orally by new tissue: the aboral ends were not completely closed by new tissue but were closely approximated and two of the pieces were slightly distended. Each of these pieces possessed a small group of minute marginal tentacle-buds at the extreme oral part of the

oblique surface (Fig. 4). No traces of tentacles were visible elsewhere. In the third piece the unpigmented tentacular ridge was visible at the most oral portion of the oblique surface but tentacle-buds had not yet appeared.

Controls. *A.* Closed and distended: marginal tentacle-buds just appearing on the whole circumference; slightly less advanced than the most oral portion of the two experimental pieces with tentacles. *B.* Closed and more or less distended but no tentacle-buds visible.

September 19. — 7 days after section. Experimental pieces: All closed and distended: marginal tentacles on the most oral portion of the oblique surface 2–3 mm.; from this region decreasing in length on each side, the lower three fourths to two thirds of the oblique surface still without tentacles.

Controls. *A.* Marginal tentacles 2–3 mm. about whole circumference. *B.* Marginal tentacles 1–1.5 mm. about whole circumference.

September 22. — 10 days after section. Experimental pieces: Marginal tentacles longest on upper side of oblique disc, decreasing to 0 toward lower side. In none of the three specimens are tentacles present on the lowest portion of the oblique disc: in one specimen the longest tentacles are 5–6 mm. and the circle of tentacles is nearly complete (Fig. 5); in the second the longest tentacles are 3–4 mm. and the lower one third of the disc is without tentacles; in the third the longest tentacles are 2–3 mm. and about one half of the disc is still without tentacles. This piece has been somewhat retarded throughout by irregular inrolling at the aboral end delaying closure and distension.

On the three more advanced pieces labial tentacles are appearing on the upper one third to one half of the disc (Fig. 5).

Controls. *A.* Marginal tentacles 5–6 mm. about whole circumference. *B.* Marginal tentacles 3–4 about whole circumference.

September 26. — 14 days after section. Experimental pieces: In the most advanced piece (Fig. 6) the longest marginal tentacles on the upper side of the disc are 10 mm., the shortest on the lower side 2 mm. Labial tentacles are present on the upper two thirds of the disc, the longest being 3–4 mm. (Fig. 6).

In the second piece the tentacles are equal in length to those of the first and show a similar arrangement.

In the third (delayed) piece the longest marginal tentacles on the upper side of the disc are 8–9 mm. while on the extreme lower portion only minute buds are present. Labial tentacles are present on the upper half of the disc, the longest being 2–3 mm.

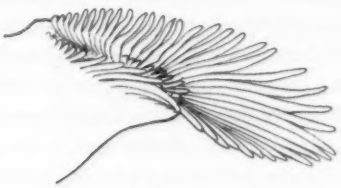


FIG. 5.

In all cases the disc is becoming less oblique (cf. Figs. 5 and 6).

Controls. *A*. Marginal tentacles 8–10 mm. about whole circumference. Labial tentacles somewhat irregular in length 1–4 mm. *B*. Marginal tentacles in one piece 8–9 mm., in other 5–6 mm. Labial tentacles in one piece 1–4 mm., in other about 1 mm.

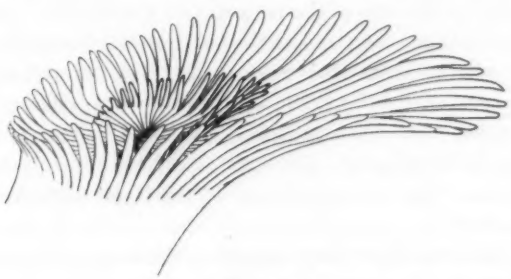


FIG. 6.

Beyond this point the controls need not concern us. The experimental pieces were observed at intervals during three weeks more. During that time there was little increase in length of the longest tentacles, but the shorter tentacles continued to grow until the asymmetry was only slight: in other words the tentacles on the upper side of the disc completed their regeneration earlier than the others. Meanwhile the disc gradually became less and less oblique until it too was almost symmetrical in position. In all pieces the obliquity of the disc was much less

when the animal was distended and oriented in the characteristic position with oral end uppermost than when it was strongly contracted. In the later stages the disc did not appear at all oblique except in the contracted condition.

The rates of regeneration in the three experimental pieces were slightly different owing to the delay in closing in some, but if we take the most advanced of these pieces and compare it with the two controls it is seen that there is a marked difference between the lower portion of the disc in the experimental piece and the controls *B*. In the controls *B* the tentacles were 1–1.5 mm. seven days after section and must therefore have appeared on the sixth day, since they were not distinct on the fifth day. In the most advanced experimental piece the tentacles had not appeared on the lowest portion of the disc on the tenth day after section; four days later, however, they were about 2 mm. in length and must therefore have appeared about the twelfth day. There is then a delay of about six days in the appearance of the marginal tentacles on the lowest part of the oblique disk as compared with the time of appearance of the tentacles on a transverse disc at the same level of the body, and in the other experimental pieces the delay is still greater. It is evident then that the retardation in tentacle regeneration on the lower portion of an oblique piece is much greater than the retardation due to differences of level in transversely cut pieces. The data of the experiment and Figs. 5 and 6 show that the appearance of the labial tentacles is similarly delayed.

As regards the time of appearance of the marginal tentacles on the uppermost portion of the oblique disc and on the control pieces *A*, the fact that tentacles appeared in the most advanced experimental piece in three days, while in the controls they appeared somewhat later, indicates that tentacle regeneration is probably slightly accelerated in the upper portion of the oblique discs. According to my notes this is the only case observed in all of my experiments in which tentacles appeared in three days. It is barely possible that the oblique cut in this piece passed so far orally that small stumps of a few tentacles remained. In view of this possibility little stress can be laid on the apparent acceleration in tentacle-regeneration in this one piece, and unfortunately

I have at present no further evidence upon this point, as my attention was not directed to it early enough. I am inclined to believe, however, that there may be a slight acceleration here, provided the inrolling of the margins is not so irregular that closure is delayed, as is frequently the case in oblique pieces.

Leaving this point for future experiments to decide, the retardation of regeneration on the lower portions of the oblique discs is sufficiently evident and requires explanation. In the course of my experiments several other pieces were cut obliquely and always with the same result, viz., appearance of the tentacles first on the uppermost portion of the disc and from this region on each side in succession toward the lowest portion. The tentacles on the lowest portion always appeared later than in transversely cut pieces at the same level.

As in the case of typical regeneration from a transverse cut surface, the presence or absence of a cut aboral end and the plane of the cut if present do not affect the oral regeneration except in so far as irregular or delayed closure of the aboral end may delay distension.

It is difficult to conceive any reason for this retardation of regeneration in the organic relations of parts of the oblique piece. Why should there be any difference between a portion of an oblique disc and a transverse disc at the same level of the body? Yet tentacle-regeneration on the former requires about twice as much time as on the latter.

The only plausible reason for this difference that has occurred to me thus far is the difference in the relation between the inrolled margin and the circulatory currents in the oblique and transverse pieces. It is evident, I think, that as soon as the oblique piece becomes closed by new tissue, and distension and stretching of the body-wall occurs, the chief tension upon the inrolled margins will coincide in direction with the plane of the disc. Thus on the lowest portion of the oblique disc the direction of tension will be obliquely upward and on the highest portion it will be obliquely downward. The result is that at the lowest portion of the margin the disc forms an obtuse angle with the body-wall, while on the opposite side the angle is acute; between these points the angle varies between these limits. Examination of the specimens

shows this condition very clearly. At the uppermost portion of the disc the body-wall bends over sharply, almost as if actually folded, while the lower margin of the disc is rounded (Figs. 3 and 4) and the angle is much less.

It is evident that circulatory currents passing orally along the inner surface of the body-wall will exert much less pressure on the lower side than on the upper side, since the obtuse angle between disc and body-wall at the lower margin deflects them and permits escape toward the central portions of the body, while at the upper portion of the margin the currents strike an acute angle. On intermediate portions of the disc the angle, and consequently the pressure exerted, vary with the position from the maximum at the upper margins to the minimum at the lower margin. It is clear, moreover, that the angle between body-wall and disc at the lowest part of the margin of the oblique disc is greater than that between the body-wall and a transverse disc, while at the upper margin it is less. Half way between the upper and lower oblique margins it is the same as in the transverse disc.

If there is any relation between the circulatory currents and tentacle-regeneration we might expect acceleration of regeneration at the upper margin and retardation at the lower margin of the oblique disc. The retardation of regeneration is very evident, but as regards acceleration the data are insufficient to permit definite conclusions, though there are indications of a slight acceleration. In any case we could not expect the acceleration to be as great as the retardation since in ordinary cases of regeneration the inrolled margin forms a more or less acute angle with the body-wall and a difference in the size of this angle would make little difference in the pressure so long as the angle remains acute. As soon as the angle becomes obtuse however, the pressure must be reduced and as the angle increases the pressure becomes less.

In this, as in other cases, the regeneration of the labial tentacles proceeds in the same manner and sequence as that of the marginal tentacles, though much more slowly. As has already been mentioned, however, I do not know whether there is any localization of pressure in the regions where these tentacles appear.

My suggestions regarding the possible rôle of local pressure in bringing about the characteristic result in oblique pieces should be considered merely as an attempt to indicate how differences of local pressure may be effective here. The hypothesis must be applied to as many cases as possible before definite conclusions are reached. For the labial tentacles my data concerning local pressure are incomplete, as was pointed out in a previous paper ('04*b*). At present, however, I do not see any other probable explanation of the delay in the regeneration of the marginal tentacles on the lower portion of an oblique disc than that suggested above.

The gradual equalization in the length of the tentacles and the gradual reduction in the obliquity of the disc which are always features of the later history of oblique pieces, lead toward the establishment of symmetry and the typical form. Is there any satisfactory interpretation of these changes or must they be regarded for the present as inexplicable? They resemble in character certain of the phenomena which have led Driesch to assume the existence of an autonomistic principle or entelechy governing form. But I am convinced that an interpretation of an entirely different sort is possible.

In the first place it is necessary to recognize that the equalization of the tentacles and the reduction in obliquity of the disc are two wholly distinct phenomena due to wholly different factors. The equalization in length of the tentacles is the result of the same factors which cause the regeneration of tentacles of a certain length in typical transverse pieces and which bring about approximate equality in the length of tentacles in normal animals. If internal pressure plays a rôle in the latter cases, undoubtedly it is equally important in the former. Considering the oblique pieces, it is clear that as soon as the tentacles on the lowest part of the margin begin to grow conditions for their further growth are similar, as regards internal pressure and circulatory currents, to the conditions on the opposite margin. Each tentacle-bud forms a blind sac whose walls are growing tissue. Conditions of internal pressure in this sac do not differ on different parts of the margin, whatever the angle between disc and body-axis. The appearance of the tentacle-buds is delayed upon the lowest part

of the margins and the possible cause for this delay has been indicated above.

If the length of the tentacles is dependent upon internal pressure, either general or local, there is no reason why the tentacles on the lowest part of the margin should not finally attain the same length as those on the highest part. They will attain this length later than the others because the first stages in their regeneration are delayed. Other factors such as the difference due to difference in level (see Child, '03*b*) may prevent the complete equalization in length, but there is always a close approximation to equality. Evidently then this regulative process does not differ essentially from others which have been discussed. The same principles which were applied to those are applicable here. In fine, the equalization in length of the tentacles is exactly what might be expected if internal pressure is the chief factor in determining their length.

The equalization of the tentacles presupposes nearly equal growth in the tentacular region on all parts of the circumference but the reduction in obliquity of the disc is apparently a compensatory process. Either the body-wall beneath the lower portion of the disc must undergo increase in length, or the body-wall beneath the highest portion must undergo decrease in length, or finally, both these changes must occur in order that the disc may attain a position at right angles to the longitudinal axis. No consideration of the conditions of internal pressure will, in my opinion, afford any means of explaining this compensatory regulative change. On the other hand I think there is little doubt that it is the result of certain characteristic activities of the animal, viz., its orientation in space. Loeb ('91) called attention to the remarkable power of orientation in *Cerianthus* and showed that in whatever position it was placed the effort was made to bring the longitudinal axis or at least its oral portion into a vertical position, and that having once attained this position the animal remains quiet until other stimuli bring about movement. My own observations agree fully with Loeb's as regards this point. The ability of pieces lying on the flat bottom of aquaria to bend the body at right angles and so lift the oral portion into a vertical position is most striking and has formed a

constant feature of my experiments. In pieces with oblique discs an interesting modification of this orienting reaction has been observed. The oral portion of the body was brought into a vertical position and furthermore the effort was made by means of unequal contraction of the muscles on the two sides of the body to bring the disc into a horizontal position at right angles to the longitudinal axis. During the earliest stages of regeneration the pieces never react normally but after they become closed and distended the reactions gradually appear. In the oblique pieces this reaction is already very distinct at the stage of Fig. 5. When the pieces are left undisturbed they orient themselves so that the disc appears nearly horizontal and the body below it nearly vertical. That the muscles of the two sides must be unequally contracted is evident. A sudden tactile stimulus or other irritation causes a marked change in the relation of parts. The specimens undergo sudden contraction and the obliquity of the disc increases greatly. The stronger the stimulus and consequently the more complete the contraction of the muscles the greater the obliquity of the disc in such cases. Left to themselves, the animals gradually extend, become filled with water again and resume the former position. The increase of the obliquity of the disc in the contracted condition results from the difference in the degree of contraction at different points of the circumference in the distended oriented condition. A brief consideration will be sufficient to render this clear; in the normal animal a stimulus of this kind causes an equal degree of contraction in all the longitudinal muscles and there is no reason to suppose that the effect is different in the oblique pieces. The increase in the obliquity of the disc which accompanies contraction in oblique pieces must result from a difference in condition of the muscles on the opposite sides of the body. If for instance we suppose that the muscles of the body beneath the highest part of the oblique disc are partially contracted in the effort to bring the disc into a horizontal position it is evident that these muscles will contract less in consequence of the sudden stimulus than those on the opposite side of the body and consequently the angle between disc and longitudinal axis must decrease.

During the earlier stages of regulation the animal is unable to

bring the disc into a completely horizontal position : it always remains somewhat oblique. Contraction at this stage causes the angle between disc and axis to approach its original value, *i. e.*, the disc becomes nearly as oblique as the original cut surface. As time goes on, however, the oriented animal brings the disc more and more nearly into the horizontal position and the obliquity of the disc in the contracted condition gradually decreases. In the later stages the obliquity is visible only in the contracted condition, the disc being apparently at right angles to the longitudinal axis in the distended oriented specimen.

This relation between the distended, oriented condition and the contracted condition is characteristic not only for pieces with oblique discs but for various other forms artificially produced. Whenever the artificial form interferes with the orientation a gradual compensatory regulation may be observed.

The most obvious conclusion and, I think, the correct one, regarding the regulation of the oblique discs is that the changes in the body-wall of the two sides of the body occur in consequence of the characteristic functional condition of the muscles. The muscles beneath the upper side of the disc being continually more or less contracted undergo a "functional" change in structure and lose a part of their original power of extension, while the muscles beneath the lower edge of the disc, being continually highly extended lose to some extent their original power of contraction. Or, considered from another point of view, there is functional atrophy on one side and functional hypertrophy on the other. The ectoderm and the entoderm of the body-wall follow these changes by similar growth or reduction. With each change further change becomes possible until the animal is finally able to orient itself in the typical manner, or in other words has attained the typical form. The most important point in this interpretation is the rôle played by the efforts of the animal to carry on its typical activities. In my opinion these efforts are the cause of the regulation. The animal attempts to perform certain acts and certain resulting conditions of the tissues give rise to a certain form. The reaction or attempt at reaction produces the form incidentally. The typical form is then in this sense the result, not the cause of the typical reaction.

No attempt at general application of this conclusion to morphology need be made at present, though the field for speculation is most attractive. I desire merely to call attention to the fact that this regulative process belongs in the same category with the changes in form of pieces of *Stenostoma* in consequence of the attempts of these pieces to carry on their typical movements (Child, '02, '03). In both cases the form is, speaking broadly, the result, not the cause of the behavior.

The Regeneration of Pieces from the Œsophageal Region.

Pieces with the oral cut surface at some level of the œsophageal region of the parent specimen and the aboral end at a greater or less distance below the œsophagus differ from pieces cut wholly aboral to the œsophagus only as regards rapidity of regeneration. In such pieces, containing a part of the œsophagus, the cut oral end of this organ unites with the cut body-wall and thus a functional mouth is formed within a day or two after section. Consequently such pieces become fully distended earlier and the tentacles appear somewhat sooner than in pieces in which a new mouth is regenerated.

In pieces representing only the œsophageal region or part of it (Fig. 7) the result usually differs widely from the preceding. In such pieces the cut ends of the œsophagus usually unite both orally and aborally with the cut body-wall and the œsophagus forms a tube extending completely through the piece and open at both ends to the exterior. Fig. 8 represents a longitudinal section of such a piece : in order that the œsophagus and body-wall may be readily distinguished in the diagrams the thin muscular layer of the former is not indicated. In these pieces there is no connection between the œsophagus and the enteron ; water passing into the oral end of the œsophagus simply passes out again at its aboral end. Each intermesenterial chamber is thus shut off from all communication with the exterior and with adjacent chambers.

As regards tentacle-regeneration these pieces follow the usual course during the first few days, becoming more or less distended with fluid, which is secreted into the enteric cavity or diffuses

through the body-wall. The body-wall becomes thinner at the oral end (Fig. 9) and tentacle-buds appear (Fig. 10), but these usually do not develop beyond the stage shown in Fig. 10. Occasionally they reach a length of 2–3 mm., but further than this their development never proceeds. The distension gradually decreases again after a week or two and the tentacles which

FIG. 8.

FIG. 9.

FIG. 7.

FIG. 10.

FIG. 11.

FIG. 12.

FIG. 13.

FIG. 14.

FIG. 15.

had attained a length of 2–3 mm. decrease in size to mere buds. In cases where the tentacles never develop beyond the stage represented in Fig. 10 they are scarcely visible at all after two or three weeks.

In some pieces, however, closure of the aboral end occurs sooner or later. This result may be attained in either of two ways. In one case the aboral cut surfaces of the œsophagus and body-wall fail to come into contact (Fig. 11) and the aboral end closes in the usual manner by union of the cut surfaces of the body-

wall leaving the aboral end of the œsophagus free in the enteron (Fig. 14). Such pieces do not differ essentially from pieces in which the aboral end lies below the œsophageal region. They become distended in the usual manner and regenerate typically, but more rapidly than pieces in which regeneration of mouth and œsophagus occurs.

In the other case the cut surfaces of body-wall and œsophagus unite in the manner described above (Fig. 8), either completely or on a part of the circumference. Then it may happen that different portions of this region of growing tissue are brought into contact as in Fig. 12. The result is the union of all these parts and so the closure of the aboral end (Fig. 13). The connection between the œsophagus and body-wall is soon broken as the piece becomes more fully distended and the condition represented in Fig. 14 is attained. From this stage on regeneration at both ends proceeds in the typical manner. In some cases this closure of the aboral end and loss of connection between œsophagus and body-wall does not occur at first, but later the margins of the body-wall happen to come into contact perhaps in consequence of the gradual decrease in distension mentioned above as following the first increase, and thus closure occurs and is followed by renewed distension and rapid regeneration. Apparently the new tissue retains the power of making new unions for a considerable time after the cut surfaces of body-wall and œsophagus appear to be firmly united.

The final result in all œsophageal pieces in which the aboral end succeeds in closing aboral to the œsophagus is typical regulation with well-developed tentacles at the oral end and several millimeters of new tissue at the aboral end.

The data of a few experiments will serve to indicate the uniformity of results. In all cases *C. solitarius* was used.

Series 30.

September 28, 1902. — Seven œsophageal pieces were prepared from large specimens in good condition as follows: at the oral end of each animal a transverse cut was made through the disc at such a level that the marginal tentacles and margins of the disc were removed and the labial tentacles were cut off near their

bases leaving stumps 1 mm. or less in length. Then a second cut was made through the œsophageal region near its aboral end. In the distal pieces thus formed the œsophagus extends from end to end of the piece, cut surfaces being present at each end (Fig. 15).

October 1. — 3 days after section. In all cases the cut margins of œsophagus and body-wall have united both orally and aborally in the same manner as in Fig. 8. All pieces are more or less distended and the oral margins slightly crenated in correspondence with the intermesenterial chambers.

October 4. — 6 days after section. All pieces with marginal tentacles, varying in length in different pieces from mere buds just visible to 2 mm.: labial tentacles still short stumps.

October 7. — 9 days after section. In two pieces the aboral end has closed as in Figures 12–14: these pieces fully distended; one with marginal tentacles 5 mm.; labial tentacles about 2 mm.; the other with marginal tentacles 3 mm., labial tentacles 1–1.5 mm.

In the five remaining pieces no aboral closure has occurred; the distension has decreased; the marginal tentacles have increased in length, though very slightly, since the previous examination, varying from minute buds to 1–2 mm.

October 15. — 17 days after section. One of the pieces which closed aborally with marginal tentacles 8–10 mm., labial tentacles 5–6 mm. At aboral end new tissue 1–2 mm.

The other closed piece was lost.

In none of the five remaining pieces has tentacle-regeneration proceeded since the previous examination. All appear almost completely collapsed and the tentacles are reduced to mere buds in all, being scarcely visible in some. One piece has begun to break up.

During the following two weeks the five pieces which did not close broke up into small pieces and died, a frequent occurrence in small pieces in which closure and regeneration do not occur. The one closed piece remained in good condition.

The difference between the piece that closed and the other five is striking. None of these five pieces ever regenerated marginal tentacles more than 1–2 mm. in length, and practically no regeneration of labial tentacles occurred. Yet the one piece which

closed while no longer than these and differing from them only in that the œsophagus communicated with the enteron, regenerated marginal tentacles 8–10 mm. in length and labial tentacles 5–6 mm. and produced new tissue at the aboral end.

Series 32.

October 1, 1902. — Seventeen œsophageal pieces were prepared (Fig. 7) the distal cut being in this case slightly more aboral than in Series 30 (Fig. 15) so that both marginal and labial tentacles and most of the surface of the disc were removed.

During two weeks these were examined several times. In all pieces the cut margins of œsophagus and body-wall united both orally and aborally and in none did the closure of the body-wall across the aboral end occur. All of the pieces became slightly distended during the first few days and marginal tentacles appeared as minute buds less than 1 mm. in length. In no case did regeneration proceed beyond this stage: labial tentacles never appeared. At the end of two weeks some pieces were beginning to break up.

Series 47.

November 7, 1902. — Nine œsophageal pieces were prepared in the same manner as those of Series 32.

November 10. — 3 days after section. Still more or less completely collapsed: no tentacles visible on any.

November 12. — 5 days after section. One piece closed aborally, and well-filled with water; marginal tentacle-buds 0.5–1 mm. In the remaining eight pieces œsophagus and body-wall have apparently united both orally and aborally: these pieces are only slightly distended and show a slight crenation of the oral margin corresponding to the intermesenterial chambers.

November 20. — 13 days after section. During the interval since the last examination seven pieces closed aborally across the end of the œsophagus. These are fully distended and bear marginal tentacles 2–3 mm.; labial tentacles just appearing.

In two pieces the œsophagus remained open aborally. These are not fully distended and the marginal tentacles are minute buds about 0.5 mm.; labial tentacles are absent.

December 2. — 23 days after section. In the seven closed

pieces regeneration has proceeded in the typical manner; marginal tentacles 5–6 mm.; labial tentacles 2–3 mm.

In the other two pieces regeneration has proceeded no further. They are still only slightly distended and with minute tentacle-buds.

In this series a larger proportion of the pieces closed aborally across the end of the œsophagus than in any other series of this kind. The date of this series was later in the year than that of any other, *i. e.*, the temperature of the water was lower and the distension of the pieces occurred much more slowly (see Child, '03*b*). It is probable that different parts of the aboral cut surfaces of the body-wall remained in contact for a longer time than in the other cases where distension occurred more rapidly, and that this prolonged contact made union possible in a greater number of cases than in other series. Other conditions such as difference in the degree of contraction of body-wall and œsophagus at the time the lower cut was made may have aided in bringing about this difference. However that may be, the point of chief importance, viz., the difference in regeneration between those pieces which did close aborally across the œsophagus and those which did not is as clear in this series as in others.

While the general result of these experiments is sufficiently clear special attention may be called to certain points.

In all cases in which the œsophagus remains open aborally and consequently does not communicate with the enteron the pieces never become fully distended and regeneration is slight. Pieces cut below the œsophageal region become well distended and the marginal tentacles may attain a length of 2–3 mm. before the mouth is formed. In my first paper ('03*a*) diffusion of water through the body-wall in consequence of the presence of soluble products of metabolism or other substances in the enteron was suggested as a possible cause of this first distension. It is also possible that secretion of fluid into the enteron occurs. In the œsophageal region the entodermal layer is thinner and undoubtedly of less functional importance than in the region aboral to the œsophagus, and it is reasonable to suppose that the accumulation of fluid in the œsophageal pieces would be much less rapid than in pieces from regions aboral to it. If this be

admitted it follows that less water would enter these pieces and less distension would occur than in pieces aboral to the œsophagus. If the internal pressure affects tentacle-regeneration, less regeneration would occur in consequence of this slight distension in œsophageal pieces than in others where distension is greater, and this is actually the case.

It was noted that the pieces in which the œsophagus remains open aborally gradually collapse again in the course of a week or two. This collapse is probably due to a slow loss of the fluid which first caused the distension. If the body-wall is slightly permeable for substances in solution in the enteron the distension produced at first will gradually diminish since in consequence of continued starvation the amount produced gradually decreases. Whatever the exact nature of the process may be, a decrease in the distension occurs. As this process continues the regenerating tentacles also decrease in size instead of continuing to grow. This fact is important as showing the apparent close relation between tentacle-regeneration and internal water-pressure. In pieces cut below the œsophagus the regeneration of the mouth and the entrance of water through it serves not only to prevent decrease in the internal pressure but to increase it, and further growth of the tentacles takes place.

The most striking feature of the experiments is the difference in behavior as regards regeneration between the pieces in which the body-wall closes aborally across the œsophagus and those in which the œsophagus remains open aborally to the exterior. The pieces of the first kind begin to regenerate typically as soon as the closure occurs, while the others never produce anything more than marginal tentacles 1–2 mm. in length. In the introductory description of these experiments it was shown that in case of closure the connection between the aboral end of the body-wall and the œsophagus is severed and the œsophagus opens into the enteron (Figs. 12–14). The breaking of this connection, *i. e.*, the change from the condition shown in Fig. 13 to that of Fig. 14 is probably itself due at least in part to internal water-pressure, though the manner of its occurrence cannot be observed. Other factors, such as a difference in rapidity of growth or a difference in resistance between the tissue of the

œsophagus and that of the body-wall may also play a part in the result. Whatever be the cause, the result is free communication between a fully formed œsophagus and the small enteric cavity with its intermesenterial divisions. If entrance of water through the œsophagus serves to maintain internal pressure in *Cerianthus* it is clear that in these pieces the pressure should at once become about equal to the pressure in a normal animal since the mouth opening and œsophagus are not regenerated structures but parts of the parent body and of full size. If internal water pressure affects regeneration we might expect in these pieces rapid regeneration, even more rapid than in pieces with regenerating mouth and œsophagus. Close comparison of these pieces with others in which mouth and œsophagus are formed by regeneration is difficult, since in the œsophageal pieces regeneration may be at first delayed until the aboral closure is complete, but the piece in Series 30 in which closure of the aboral end occurred between October 4 and October 7 and by October 15 the marginal tentacles were 8–10 mm. and the labial tentacles 5–6 mm., show the rapidity of regeneration. In fact regeneration in this piece after closure is more rapid than in any other case noted in my records with the exception of other pieces of the same kind.

The striking difference between œsophageal pieces in which the aboral closure occurs and those in which it does not constitutes evidence of great importance for the influence of internal water-pressure on regeneration. As regards the influence of local pressure due to circulatory currents in determining the position of tentacles and in their regeneration these experiments afford no direct evidence. They show merely that the greater the distension of the piece and consequently the more widely open the intermesenterial chambers and the greater the force and volume of the circulatory currents the more rapid is regeneration.

Summary.

1. In pieces with oblique oral end the rapidity of tentacle regeneration differs on different parts of the disc, being greatest on the uppermost (most oral) portion and least on the lowest (most aboral) portion. The delay in regeneration on the lowest portion

as compared with the highest portion is much greater than the difference in rapidity of regeneration due to difference in level.

2. The only reason apparent for the difference in rapidity of regeneration on different parts of oblique discs is the difference in the angle between disc and body-wall, which is acute on the upper side of the disc while on the lower side it is obtuse. In consequence of this difference the local pressure exerted by the circulatory currents passing orally in the intermesenterial chambers must be much greater on the upper side of the disc than on the lower. If regeneration is influenced by these currents we should expect delay on the lower side, and it occurs in all cases.

3. The later equalization in length of the tentacles in pieces with oblique discs is due to the conditions which bring about equality in length of tentacles in normal animals. After the appearance of the tentacles the conditions as regards internal pressure are essentially similar on all parts of the oblique margin and equalization must be expected if the length of the tentacles is determined by internal pressure.

4. The reduction in the obliquity of the disc in oblique pieces is a compensatory process resulting from the attempt of the animal to orient itself with longitudinal axis vertical and disc horizontal. In the attempt at orientation unequal contraction of the muscles on different parts of the circumference occurs, and its continuation brings about changes in the tissues which lead gradually toward the establishment of the typical form. The form is the result, not the cause of the reaction.

5. In pieces cut wholly within the œsophageal region the two cut ends of the œsophagus usually unite with the cut ends of the body-wall, thus leaving the œsophagus open to the exterior at both ends. This method of closure isolates each intermesenterial chamber completely and prevents any direct communication between the enteron and the exterior.

6. Such œsophageal pieces become slightly distended at first in consequence of diffusion of water through the walls, but since the œsophagus is not in communication with the enteron the internal pressure remains far below that of the normal animal. Regeneration of the marginal tentacles begins in such pieces, but never proceeds beyond the formation of mere buds.

7. Occasionally an œsophageal piece closes aborally by union of the body-wall across the end of the œsophagus. In these cases communication between the œsophagus and enteron is established, the piece becomes fully distended, and regeneration proceeds in the typical manner.

8. The difference in regeneration between the "closed" and "open" œsophageal pieces is undoubtedly due to the difference in the degree of internal water-pressure.

HULL ZOÖLOGICAL LABORATORY,
UNIVERSITY OF CHICAGO, November, 1903.

BIBLIOGRAPHY.

Child, C. M.

'02 Studies on Regulation, I. Fission and Regulation in Stenostoma. Arch. f. Entwickelungsmech., Bd. XV., H. 2, 1902.

'03 Studies on Regulation, II. Experimental Control of Form-Regulation in Zoöids and Pieces of Stenostoma. Arch. f. Entwickelungsmech., Bd. XV., H. 4, 1903.

'03a Form-Regulation in Cerianthus, I. The Typical Course of Regeneration. Biol. Bull., Vol. V., No. 5, 1903.

'03b Form-Regulation in Cerianthus, II. The Effect of Form, Position, Size, and Other Factors upon Regeneration. Biol. Bull., Vol. V., No. 6, Vol. VI., No. 1, 1903.

'04a Form-Regulation in Cerianthus, III. The Initiation of Regeneration. Biol. Bull., Vol. VI., No. 2, 1904.

'04b Form Regulation in Cerianthus, IV. The Rôle of Water-Pressure in Regeneration. Biol. Bull., Vol. VI., No. 6, 1904.

'04c Form-Regulation in Cerianthus, V. The Rôle of Water-Pressure in Regeneration: Further Experiments. Biol. Bull., Vol. VII., No. 3, 1904.

PORTABLE ANT-NESTS.

ADELE M. FIELDE.

Portable ant-nests, constructed by me in the summer of 1900, were described in BIOLOGICAL BULLETIN, No. 2 of Vol. II., which is now out of print. Improvements that have since been made in them, and their present use by myrmicologists in America, Europe and Africa, justify a new statement of the method of making them. I have now ants that have lived in them, without earth, for three years, in health and apparent contentment.

The floor of the nest is a pane of double-thick, transparent glass. This is laid upon very thick, white blotting paper, giving an elastic bed to the pane of glass and the best background for observation of the ants. The paper has just the area of the glass, but is not fastened thereto.

The outer walls of the nest are laid a quarter inch, or six millimeters, from the edge of the pane. They consist of two strips of double-thick glass, a half inch, or thirteen millimeters, wide, the one strip superimposed on the other. Both are held in place by crockery cement.[1] The wall is smoothly laid up, with no interstices where an ant may hide or escape.

The partitions are double the width of the wall, which they otherwise copy. At one end of every partition a space is left whereby the ants may pass from room to room. This passage-way is covered by a thin celluloid film or a piece of mica. It is desirable that this covering be transparent, so that the passage-way underneath it may be scanned from above, on lifting the end of the toweling which is to overlay it.

After the cement is well dried, the edge of the floor-pane and the outside of the walls are covered with a fabric impervious to light. Cloth serves better for this purpose than does paper, the edges of the nest being subject to much handling. Le Page's or

[1] The use of cement instead of glue was recommended by Dr. W. M. Wheeler. Diamond, Major's or any reliable kind may be used. I have merged in water, for two weeks, a nest constructed with Major's cement, without loosening its parts. The directions accompanying the selected cement should be followed

some other good liquid glue is used for securing the fabric upon the walls.

The walls and partitions are topped by Turkish toweling of a sleazy sort, folded over one layer of cotton wadding so that the edges of the strip of toweling meet in the center of the under side of the wadding. The wadding is cut to the same width as the wall or the partition. The toweling is just twice the width of the wadding, and its edges are basted evenly together, making a cushion of even thickness. It serves the double purpose of admitting air into the nest and of preventing the escape of the ants between the roof and its supports. It is held taut and is made level; is fitted snugly at the corners; exhibits no ravelings to afflict the ants; and is firmly glued to the glass beneath it. When a cushion becomes soiled by long use of the nest, the glue may be softened by soaking and the cushion may be removed and be replaced by a new one. The ends of the cushions are fringed out a half inch or more, and are left open so that the enclosed wadding may be adjusted to present a perfectly level surface.

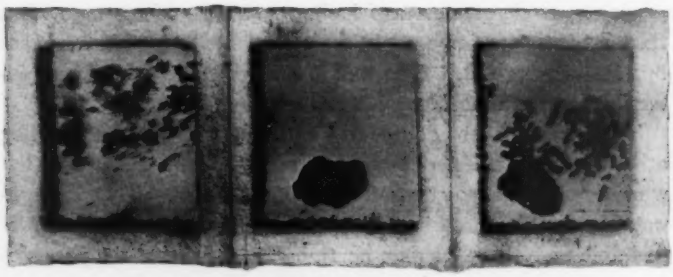
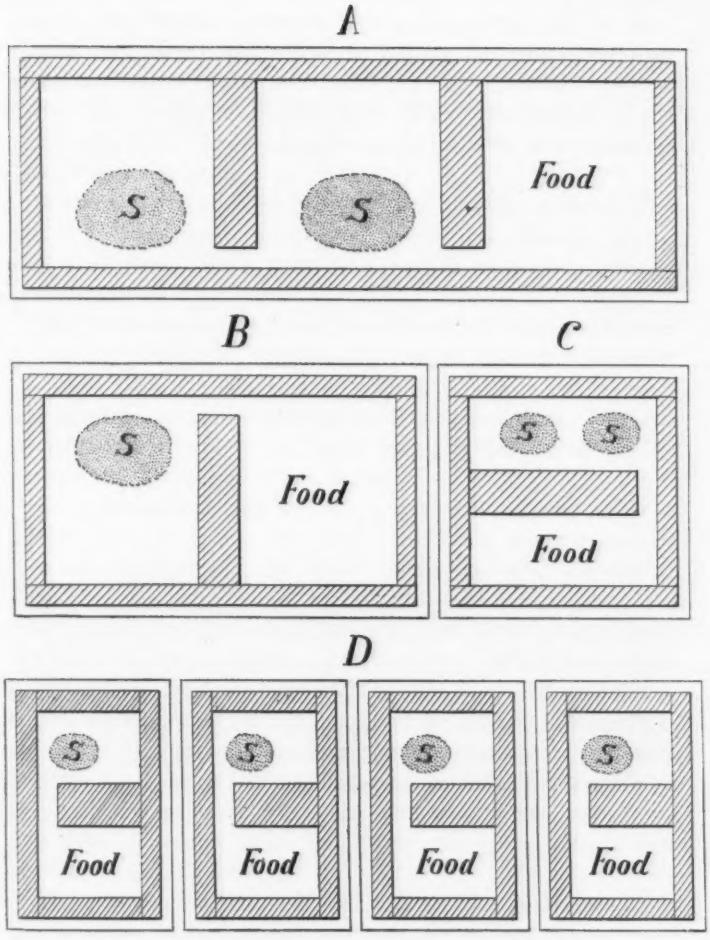


FIG. 2. The A nest completed.

There is a glass roof-pane for each room in the nest. The glass is thin; extends to the middle of the partition and to the outer edges of the walls on which it rests; prevents the exit of ants; and permits observation of their behavior. The glass may be without color, or it may be of a red or orange tint that will partially exclude ultra-violet rays of light. Ants perceive only such rays of light as are of short wave-length and, by use of a spectroscope, a glass roofing may be selected which renders the



Bases of Seven Ant-nests, Filling Three Shelves of Portable Case.

FIG. 1.

ants visible within the nest while it protects them from such light-rays as they instinctively shun.[1] If such glass is used for roofing the nest, the ants will behave as if in the darkness where they habitually live.

An outer roofing of blotting-paper makes the interior of the nest wholly dark. The food-room should be light, as it represents the ant's outside world.

When any room in the nest requires cleaning, it is covered only with transparent glass, and then the ants withdraw from it with their young into a dark room, which may in its turn be made light.

The food-room is dry, and in cool weather requires attention but once a fortnight. Sponge-cake merged in a little honey or molasses, banana, apple, mashed walnut, and the muscular parts and larvæ of insects are among their favorite edibles. Food is constantly attainable in the nest, but it is introduced in tiny morsels that it may not vitiate the air.

Since moisture encourages the growth of mold, no water is put into the food-room. But ants often drink, and they require a humid atmosphere. All other rooms than that allotted to their food are made humid by laying a flake of sponge on the floor and keeping the sponge saturated with clean water dropped twice a week from a pipette. The proportion of the floor which is covered by the sponge depends on the degree of moisture in the soil usually chosen as the habitat of the species. The sponges are kept clean by weekly washing and an occasional immersion in alcohol. Sponges of fine tough texture render best service, as they offer no apertures where the ants may conceal their eggs. The flake of sponge is so thin as to permit the ants to pass between it and the roof-pane.

The completed nest is less than half an inch or thirteen millimeters in its interior height, and does not exceed three fourths of an inch or two centimeters in its exterior height. A low-power lens is easily focused upon the ants within the nest.

During four years of experimental work with ants, I have found that the nests whose bases are represented in the drawing

[1] "Supplementary Notes on an Ant," Adele M. Fielde, *Proceedings of the Academy of Natural Sciences of Philadelphia*, June, 1903, p. 492.

meet the requirements of the various species that I have desired to house for long periods.

A is	16¼	× 6	inches or	41	× 15	centimeters.
B "	10	× 6	"	25½	× 15	"
C "	6	× 6	"	15	× 15	"
D "	6	× 4	"	15	× 10	"

Nests of these dimensions fit into and fill a portable wooden case or box having an interior length of 17 inches or 43 centimeters; a width of 7 inches or 18 centimeters; and a height of 4¾ inches or 12 centimeters. It is made of half-inch pine boards, dovetailed at the joinings. The interior of the case is equally divided lengthwise into four compartments by three shelves that are supported in grooves cut in the end-pieces of the case. The shelves are a quarter inch or six millimeters thick, and they leave space at their outer edge for the inset of a door which forms the front of the case, is hung by hinges at the bottom, and is held shut by two buttons affixed to the top-piece of the case.

FIG. 3. Portable Case for the Nests.

Holes are bored in both sides of the case for the inlet of air to the enclosed nests.

A handle placed lengthwise on the top of the case permits its convenient carriage. When its four compartments are filled with

nests, its weight is less than sixteen pounds. Ants have made long journeys in my portable nests, with no grave disturbance of their domestic arrangements.[1]

When preparing the nests for a journey, tapes are tied around them, so as to hold the roof-panes securely in position, and bits of wadding are so inserted as to prevent their displacement in the case. Four of the A nests, sixteen of the D nests, or a selection from among the A, B, C and D nests may be carried in the case.

Before constructing my ant-nests, I made and used those of the Lubbock and of the Janet patterns, both much older than my own. The Lubbock nest, holding the ants on an island by a moat filled with water, is not portable; and whenever the pane of glass, covering the layer of earth over the island, needs to be cleaned, there must be a disturbance of the domestic interests of the ants. But the base of the Lubbock nest is a valuable adjunct when the ants are to be housed in my nests. It consists of a square or oblong block of wood, about two inches or five centimeters thick, with a channel grooved to half the thickness of the wood at a half inch from its edge all around. When the channel, which is an inch or more in width, is filled with water, the island thus formed serves well for the temporary confinement of ants. The ants are brought, as Janet suggested, from their wild nests in little bags permeable by air, or in jars whose mouths are covered by gauze. The contents of the bag or jar are deposited thinly upon the island; a piece of glass covered by blotting paper and raised slightly above the general surface is laid over some portion of the area; and the ants, within a few hours, gather the young underneath the darkened glass. Their progress in their work is made visible by an instant's lifting of the blotting paper. Selections from the total capture may be made for removal to the glass nests. My nests of earlier construction, like the Janet nests, had an aperture in the wall through which the ants could themselves transport their young from the earth into the glass nest. But I have found it expedient to personally make selection from the total capture rather than to allow the ants to bring their whole community into the glass nest.

[1] The photographs with which this paper is illustrated were very kindly made for me by Mr. J. G. Hubbard and Dr. O. S. Strong.

Forel's method of making, upon a table, a stockade of dry plaster of Paris, to prevent the escape of the ants deposited within it, serves well when large colonies are dealt with. But ants have high regard for personal cleanliness and are discomforted by the adhering dust which punishes their effort to escape over this stockade. The Lubbock island renders clean stock.

The Janet nest, a series of four pits in porous stone, cement or stucco, with water in the pit at the end opposite the food-pit, proved that the ants may live healthfully without earth; showed the practical value of more than one compartment in the artificial nest; and gave an excellent background for viewing the ants. But the Janet nest is cumbrous and weighty; and its food room becomes quickly mouldy in hot weather.

The glass nests are constructed at less expense than are those of either the Lubbock or the Janet pattern; they are easily kept clean, and the small space which they occupy, with their very light weight, greatly facilitates the bringing of the ants under close observation.

THE MARINE BIOLOGICAL LABORATORY OF WOODS HOLL, MASS.,
July, 1904.

EXPERIMENTS ON THE ORIGIN OF THE CLEAVAGE CENTROSOMES.

EDWIN G. CONKLIN.

(From the Zoölogical Laboratory of the University of Pennsylvania.)

The great diversity of opinion as to the origin of the cleavage centrosomes which appear during the fecundation of the egg is well known to all students of cytology. By different authors every possible view has been held with regard to the source of these centers, as may be seen from the following classification:

1. The cleavage centrosomes come from the sperm centrosome; Boveri ('87, '92, '95), Vejdovsky ('88), Fick ('93), Wilson and Mathews ('95), Hill ('95), Mead ('95), Reinke ('95), Kostanecki and Wierzejski ('96), Kostanecki and Siedlecki ('96), Sobotta ('97), MacFarland ('97), Erlanger ('97), Griffin ('99), Coe ('99), Linville (1900).

2. The cleavage centrosomes come from the egg centrosome; Van Beneden ('87), Wheeler ('95); all cases of normal and artificial parthenogenesis.

3. The cleavage centrosomes come from both egg and sperm centrosomes; Fol ('91), Guignard ('91), Blanc ('93), Conklin ('94), Carnoy and Lebrun ('99).

4. The cleavage centrosomes come from neither egg nor sperm centers but are new formations; Foot ('97), Lillie ('97), Child ('97), Mead ('98).[1]

It is probable that some of these conflicting views may be attributed to erroneous observations, and the writers who have maintained the first view have in general explained all others as due to this one cause, but on the other hand some of the evidence in favor of these other views cannot be thus lightly brushed aside. As long as this question remained on a purely observational basis no one seems to have seriously considered that there might be an element of truth in more than one of these views and that the cleavage centrosomes might arise differently in differ-

[1] For references see Wilson, "The Cell in Development and Inheritance," 1900.

ent animals or even in the same animal under different conditions.

The experiments of R. Hertwig, Morgan, Loeb and Wilson have shown that the unfertilized egg is capable of giving rise to cleavage centrosomes and spindles, while the observations of Delage, Boveri and others on merogeny have proven that a normal mitotic figure may appear in connection with the sperm nucleus in enucleated egg fragments. Under these circumstances it ought to be possible, by slightly altering normal conditions, to bring about the formation of a spindle in connection with each germ nucleus.

In the summer of 1901, while at the Marine Biological Laboratory at Woods Holl, I undertook some experiments on the eggs of *Crepidula* in order among other things to test this possibility. Since this animal is one which does not conform to the prevalent view as to the origin of the cleavage centrosomes it seemed all the more favorable for such work. As the eggs of these gasteropods are fertilized while still in the oviduct I have found it impracticable to experiment with unfertilized eggs but have worked entirely with eggs into which a spermatozoön had already entered.

The normal course of the fecundation in this animal may be briefly recalled: After both polar bodies have been extruded the egg nucleus lies at the animal pole in an area of cytoplasm while the sperm nucleus lies in the yolk near the periphery of the egg and usually near the vegetative pole. Then the egg centrosome which is left in the egg at the close of the second maturation division, rapidly disappears and in its place is left the large egg aster or sphere. At no stage is there a clearly marked sperm centrosome, but a radiating cytoplasmic figure, the sperm aster, develops in connection with the sperm nucleus and these two migrate through the yolk until they come into contact with the egg nucleus and sphere, immediately under the polar bodies. Here the egg and sperm spheres fuse and at their periphery two separate and independent centrosomes appear which ultimately come to lie at opposite poles of the first cleavage spindle. It is probable that one of these centrosomes comes from the egg sphere and the other from the sperm sphere though there is no

positive evidence that they are directly derived from egg and sperm centrosomes.

If now the eggs of *Crepidula plana* which have given off the second polar body but a short time before are brought for four hours into a 1 per cent. solution of NaCl in normal sea water

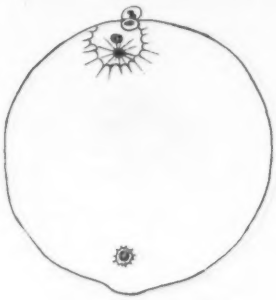


FIG. 1.

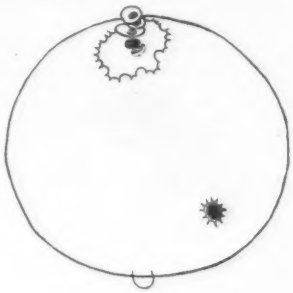


FIG. 2.

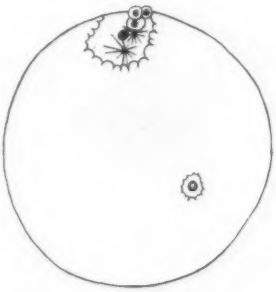


FIG. 3.

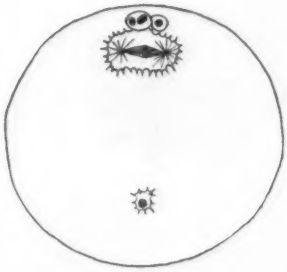


FIG. 4.

FIGS. 1–4. Eggs of *Crepidula plana* treated with 1 per cent. NaCl in sea water for four hours, viewed from the side. In all the eggs the polar bodies are at the upper pole, the egg nucleus and centrosome, or spindle, immediately below this, while the sperm nucleus lies in a small area of cyptoplasm near the lower pole. Various stages in the formation of the egg spindle are shown.

they will present the appearances shown in Figs. 1–12. These figures are camera drawings of eggs in different stages of the formation of the first cleavage spindle and all are from the same experiment.

An examination of these figures shows that various stages in the division of the egg centrosome occur (Figs. 1–5) leading to

the formation of a perfect spindle of small size. There can be no doubt that the centrosomes of this spindle are derived from the egg centrosome. The sperm nucleus is at this time far removed from the egg nucleus and is closely surrounded by yolk; no astral radiations are found in connection with it, though one

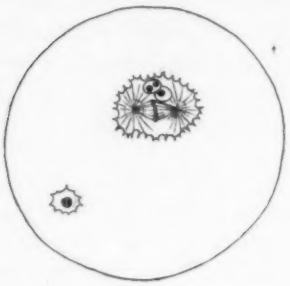


FIG. 5.

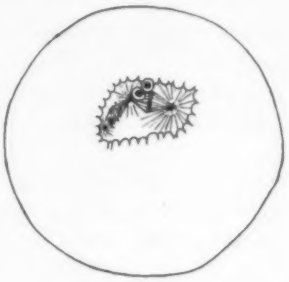


FIG. 6.

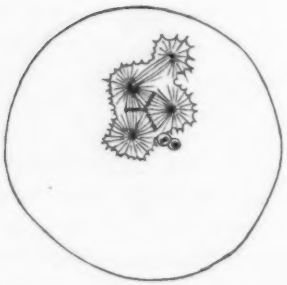


FIG. 7.

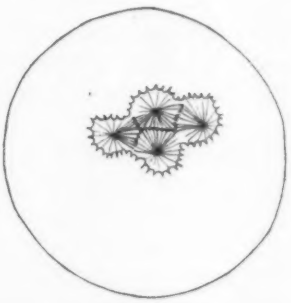


FIG. 8.

FIGS. 5–8. NaCl eggs of *C. plana* viewed from the animal pole; the two polar bodies are shown nearly over the spindles in the first three figures. In Fig. 5 the sperm nucleus is still some distance from the egg spindle; Fig. 6 shows an egg spindle and a sperm spindle joined at one pole; Figs. 7 and 8 show stages in the formation of a tetraster from the egg and sperm spindles.

or two granules which lie close to the nuclei may possibly represent centrosomes (Fig. 4).

Unfortunately a gap occurs at this stage in my material; in all the preceding figures (1–5) the sperm nucleus is small and densely chromatic and is far removed from the animal pole; in the succeeding figures (6–12) the sperm nucleus has been re-

solved into chromosomes which lie near those of the egg. In all cases there are two spindles present which are usually united into a tetraster though they may be more or less independent of each other. In some eggs yolk spherules separate the two spindles so that a tetraster is not formed (Figs. 9, 10), while in others an incomplete tetraster is formed (Figs. 6, 7); in still

FIG. 9.

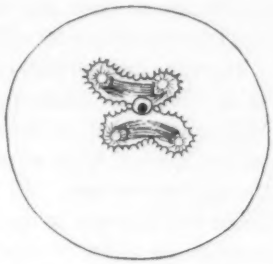


FIG. 10.

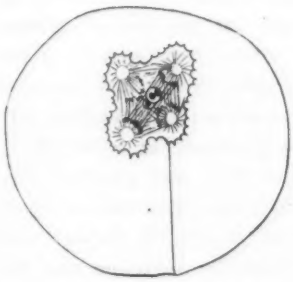


FIG. 11.

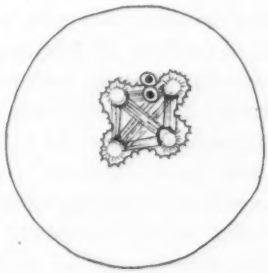


FIG. 12.

FIGS. 9–12. NaCl eggs of *C. plana*, viewed from the animal pole; the polar bodies lie above the spindles in all the figures. Fig. 9. Egg and sperm spindles united at one pole. Fig. 10. The two spindles quite separate. Figs. 11 and 12. Complete tetrasters in different phases of the separation of the chromosomes.

others the tetraster is complete, each of the four poles being united to the other three (Figs. 8, 11, 12).

Although I have not seen the genesis of the sperm spindle there seems to be no reason for doubting that it is formed essentially as the egg spindle is and that the two are at first wholly independent; only later do secondarily formed fibers connect one

or both of its poles with those of the egg spindle. Since under normal conditions one of the cleavage centrosomes of *Crepidula* arises in connection with the egg and the other with the sperm nucleus the only respect in which these experimental results differ from the normal is that in the former the centrosomes divide while the nuclei are still far apart thus giving rise to two spindles or to a tetraster, whereas in the latter these centrosomes do not appear until after the germ nuclei and spheres have met and they do not divide until the prophase of the second cleavage.

In such a case as this we have essentially the same phenomenon as is found in dispermic echinoderm eggs (Driesch, Boveri, Wilson) save that in the former the two additional centrosomes are not derived from an additional spermatozoön but come from the egg centrosome. Of this fact there cannot be a particle of doubt and it seems to me to shed light upon the much discussed question as to the source of the cleavage centrosomes of different animals under normal conditions.

It has evidently been a mistake to suppose that the cleavage centrosomes could arise in but a single way and that all animals must conform to this single type. Under experimental conditions the cleavage centrosomes may arise in one and the same animal in connection with the sperm nucleus, in connection with the egg nucleus or, as I have shown in connection with both of these nuclei, while it is possible that they may arise *de novo* anywhere in the egg cytoplasm, though this latter view is by no means so well supported by evidence as are the former ones (see Conklin 1902). It is highly probable therefore that the source of the cleavage centrosomes may differ in different animals, or even in the same animal under different conditions.

It is interesting to note that this whole discussion as to the supposed importance of the source of the cleavage centrosomes had its origin in the thought that the sex cells were in themselves incomplete and incapable of development save as each complemented the other (Boveri '87, '91), or in the rival notion that the centrosomes were the bearers of heritable qualities (Fol '91). In the light of recent experimental work both of the these views are seen to be untenable and the subject has therefore lost most of its interest and significance.